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Formalism for the Neural Network of Visual Systems

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Abstract

A formalism to describe neural interrelations is developed on the exemplary case of the fly visual system. Absolute and relative indices are employed to identify the position of neural elements within the lattices of the visual ganglia. Illustrative applications as the projection of fly retinula cell axons into the lamina are discussed as well as the general feasibility of the formalism to other visual systems.

A. Introduction

The functional properties of a neural system can be elucidated only if a clear unambiguous formalism exists for the description of the neuronal interconnections. Here we will present a formalism for the neural network in visual systems.

Especially the fly eye seems to provide an outstanding opportunity for a formal treatment because of its unusually high degree of regularity which is now generally appreciated, owing to the extensive explorations of a number of investigators (for reviews see Trujillo-Cenóz, 1972; Braitenberg and Strausfeld, 1973). After developing the scheme of description for the fly visual system, the feasibility of the formalism to other neural networks will be discussed.

B. Vector Notation for the Fly Visual Network

The fly eye can ideally be treated as a set of two dimensional lattices, since going from the periphery of the eye towards its central parts the homologous lattice structure of retina, lamina and medulla can be clearly recognized (Braitenberg, 1970). Recently we have outlined (Stavenga, 1975) that the neural lattices are (approximately) of the centered-rectangular-type. Two orthogonal axes H(orizontal) and V(ertical) can be utilized to denote the principal directions in the lattices.

Moreover the lattice points can be specified with the aid of a set of absolute indices i and j or a pair of relative indices i^* and j^*. The use of index pairs (or vectors) can be exemplified nicely on the retinula lattice (cf. Braitenberg, 1970). Figure 1 shows that we can assign to each retinula cell R_k a relative index pair (vector) $\boldsymbol{q}_k$ with $k=1$–8 so that $\boldsymbol{q}_1=(-1,-1)=(\bar{1},\bar{1})$; $\boldsymbol{q}_2=(-1,1)=(\bar{1},1)$; $\boldsymbol{q}_3=(\bar{1},3)$; $\boldsymbol{q}_4=(0,2)$; $\boldsymbol{q}_5=(1,1)$; $\boldsymbol{q}_6=(1,\bar{1})$ and $\boldsymbol{q}_7=\boldsymbol{q}_8=(0,0)$.

Within the complete retina the retinulae also can be related to each other with the aid of relative indices. In general relative positions of neurons (also in higher order ganglia) can be specified by vectors. Even the projection of neural elements onto different ganglia may be described with relative indices. As an exemplification of this statement we will treat the retina-lamina projection next.

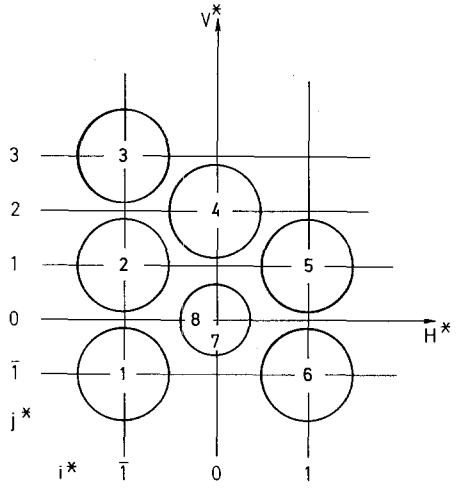

Fig. 1. The fly retinula lattice. The retinula cells, actually represented by their rhabdomeres in the distal portion of the retinula (cf. Boschek, 1971, Fig. 2), are numbered as usual from 1 to 8. (The rhabdomeres of retinula cells R_7 and R_8 are lined up with each other.) The photoreceptor cells also can be characterized with a pair of relative indices (i^*, j^*) as is indicated by the centered-rectangular-lattice lines. The principal directions are indicated by the H*-(orizontal) and V*-(ertical) axes

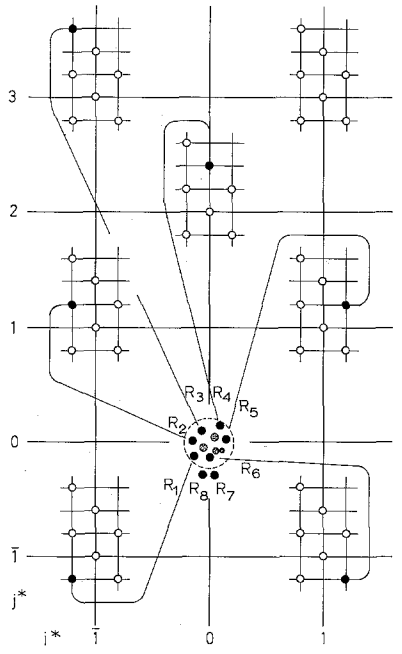

Fig. 2. Formalized projection of retinula cell axons from a conjugated set of retina-lattice elements (i.e. a set of retinulae) into the lamina lattice. Here i^* and j^* are relative indices which characterize the relative positions of the retinulae. The ommatidium $O^*(0,0)$ has been omitted to show the neuro-ommatidium $N^*(0,0)$. This lamina-lattice element receives from the ommatidia $O^*(\boldsymbol{q}_k)$ the axon of retinula cell $R_k(\boldsymbol{q}_k)$; see text for further explanation. The dotted circles indicate lamina neurons (cf. Fig. 4)

C. Formalizing the Retina-Lamina Projection in the Fly Eye

The projection of retinal axons onto the lamina has been amply discussed in articles and reviews on the neural superposition theory of fly vision (Kirschfeld, 1971; Trujillo-Cenóz, 1972; Braitenberg and Strausfeld, 1973). Diagrammatically this projection is given in Fig. 2, where a set of neighbouring ommatidia is shown, each comprising the retinula of Fig. 1. We note that henceforth an asterisk affixed to lattice elements denotes that relative index values are applied.

Then it follows from Fig. 1 that from ommatidium $O^*(0,0)$ (which is excluded for clarity's sake) the axons of sense cells R_7 and R_8 enter the neuro-ommatidium $N^*(0,0)$. (We call a neuro-ommatidium the set of neuronal elements which by spatial repetition generates the lamina; the neuro-ommatidium forms the basis of the lamina lattice.) Entering into neuro-ommatidium $N^*(0,0)$ furthermore there are the axons of those retinula cells $R_k = R_k(\boldsymbol{q}_k)$, $k = 1$–6, which are part of ommatidia $O^*(\boldsymbol{q}_k)$; e.g. towards neuro-ommatidium $N^*(0,0)$ an axon descends from retinula cell $R(\bar{1},\bar{1})$ located in ommatidium $O^*(\bar{1},\bar{1})$, et cetera.

The retina-lamina projection can be formalized in an elegant way by introducing an operator A_k^* with the property

$$A_k^*\{O^*(\boldsymbol{q}_k)\} = N^*(0,0), \quad k = 1\text{–}8. \tag{1}$$

Obviously Relation (1) can be generalized. Into neuro-ommatidium $N^*(\boldsymbol{a}^*) = N^*(i^*, j^*)$ the ommatidium $O^*(\boldsymbol{a}^* + \boldsymbol{q}_k)$ projects the axon of photoreceptor cell R_k, or

$$A_k^*\{O^*(\boldsymbol{a}^* + \boldsymbol{q}_k)\} = N^*(\boldsymbol{a}^*), \quad k = 1\text{–}8. \tag{2}$$

From the previous treatment one may appreciate the usefulness of the assignment of relative indices to cells and cell groups for characterization of relative positions of neural elements and their interconnections. Moreover, as may have been anticipated already from Eq. (2), a scheme for characterizing cells in the complete visual system can be advanced. To this we will proceed in the next section.

D. Absolute Indices

In the fly visual system a two-fold mirror symmetry can be recognized. Firstly, left and right eye are symmetrical with respect to a vertical plane through the body's long axis and secondly, one can imagine in each eye a so-called equatorial plane with respect to which upper and lower part of the eye show mirror symmetry. Regarding the (two-dimensional) retinula lattice of Fig. 1 this implies that the assigned H*- and V*-axes are reflection axes. Actually the pattern of Fig. 1 is observed from the outside in the upper half of the left eye (cf. Braitenberg, 1970, 1972).

Some obvious agreements are now called for. In all four eye quadrants the respective photoreceptor cells preserve their index pair, that is, always $R_k = R_k(\boldsymbol{q}_k)$. Furthermore the relative positions of ommatidia will be denoted with relative indices having the same sense as in the local retinula pattern. As is easily understood, the two-fold symmetry then offers no restrictions to the applicability of the retina-lamina projection formulae advanced in the previous section. Yet, these formulae can usefully be generalized by applying a pair of absolute indices: i and j.

We make the statement here, that the index i of an ommatidium has the property that $|i|$ increases going from anterior to posterior in both eyes, i being positive in the left eye and negative in the right eye. Subsequently, the index j of an ommatidium will be positive in the upper eye parts, starting with $j = 0$ for ommatidia in the first row above the equatorial plane.

The ommatidia in the lower eye parts obtain a negative j starting with $j=-1$ for the first row below the equatorial plane.

It may be noticed that with these conventions i^* and $|i|$ and also j^* and $|j|$ increase in the same directions. Hence, if $\boldsymbol{a}=(i,j)$ and $\boldsymbol{a}_{\|}=(|i|,|j|)$ the retina-lamina projection can be written, analogous to Eq. (2), as

$$\boldsymbol{A}_k\{O(\boldsymbol{a}_{\|}+\boldsymbol{q}_k)=N(\boldsymbol{a}_{\|}), \quad k=1\text{–}8. \tag{3}$$

[We drop the asterisks here because Eq. (3) employs the absolute index notation.]

The two-fold symmetry in the fly visual system can be accounted for even more advantageously. We therefore define a sign-function by

$$\begin{aligned} \operatorname{sign} x &= -1 \quad \text{if} \quad x<0 \\ \operatorname{sign} x &= +1 \quad \text{if} \quad x\geqq 0 \end{aligned} \tag{4}$$

and we conjugate the set of vectors $\boldsymbol{s}_k$ to the set $\boldsymbol{q}_k=(i_k^*, j_k^*)$ by

$$\boldsymbol{s}_k=(i_k^* \operatorname{sign} i,\ j_k^* \operatorname{sign} j), \quad k=1\text{–}8. \tag{5}$$

Then Relation (3) is equivalent to

$$\boldsymbol{A}_k\{O(\boldsymbol{a}+\boldsymbol{s}_k)\}=N(\boldsymbol{a}) \tag{6}$$

$$\boldsymbol{A}_k\{O(\boldsymbol{a})\}=N(\boldsymbol{a}-\boldsymbol{s}_k) \tag{7}$$

and

$$\boldsymbol{A}_k^{-1}\{N(\boldsymbol{a})\}=O(\boldsymbol{a}+\boldsymbol{s}_k) \tag{8}$$

for $k=1$–8.

In words, Eq. (7) expresses that from ommatidium $O(\boldsymbol{a})=O(i,j)$ the k^{th} axon enters neuro-ommatidium $N(\boldsymbol{a}-\boldsymbol{s}_k)$. The inverse operation is formalized in Eq. (8) which states that neuro-ommatidium $N(\boldsymbol{a})$ receives the k^{th} axon from ommatidium $O(\boldsymbol{a}+\boldsymbol{s}_k)$.

Equations (6)–(8) hold for all parts of the eye. Their adequateness may be valued from a treatment of a quite interesting case, i.e. the retina-lamina projection in the equatorial area, to which we turn now.

E. Retina-Lamina Projection Near the Equator

Owing to the wiring of photoreceptor axons from one ommatidium towards different neuro-ommatidia, some of these axons cross the equator as has been predicted from optical studies by Kirschfeld (1967) and proved histologically by Horridge and Meinertzhagen (1970a) and Boschek (1971). This phenomenon has been schematically presented in Fig. 3. Each square represents an ommatidium in the left eye.

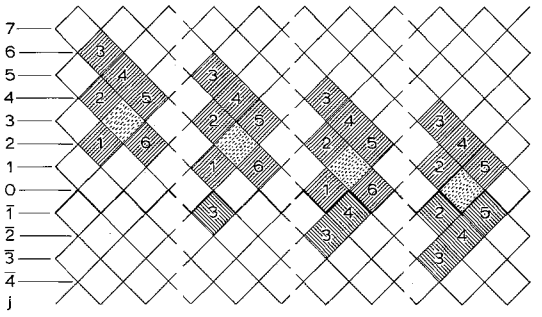

Fig. 3. Retina-lamina projection in the equatorial region of left eye. Above the (drawn) equator the retinula pattern is identical to Fig. 1. Below the equator this pattern is mirrored. The ommatidium row number is indicated by the absolute index j. Going from left to right the set of distinguished squares represents the set of ommatidia which deliver axons to a neuro-ommatidium with $j=3, 2, 1, 0$ respectively. The number in the hatched ommatidia gives the number of the retinula cell the axon of which joins the axons of sense cells R_7 and R_8 which leave the speckled ommatidium. A neuro-ommatidium having $j=2, 1, 0$ (or $-1, -2, -3$) receives axon(s) from the opposite half of the eye. The appearance of the different stages as drawn in the figure is not unlike the cornea pseudopupil phenomenon observable near the equator

We have argued above, that in general a neuro-ommatidium located in the upper half of the left eye will receive axons from neighbouring ommatidia organized in the way as shown in Fig. 3 at the left; i.e. if $N(i,j)$ has a $j\geqq 3$, then each of six neighbouring ommatidia send one axon to this neuro-ommatidium [see Fig. 2 and for instance Eq. (2)]. In Fig. 3 the number in the ommatidium represents the value k of the photoreceptor cell R_k whose axon enters the neuro-ommatidium $N(i,j)$ corresponding to ommatidium $O(i,j)$, the latter being indicated by the speckled square. [From the latter ommatidium the axons R_7 and R_8 always enter $N(i,j)$.]

However, if $j=2, 1, 0, \ldots, -3$, more than six adjacent ommatidia send an axon to the neuro-ommatidium. This peculiar behavior, shown in Fig. 3, is completely compatible with Relations (6)–(8), as is directly seen from an example: neuro-ommatidium $N(i,1)$ receives an axon with $k=3$ both from $O(i-1,\bar{2})$ and from $O(i-1,4)$ since, as follows straightforwardly from Eq. (5), $\boldsymbol{s}_3=(\bar{1},3)$ if $j>0$, but $\boldsymbol{s}_3=(\bar{1},\bar{3})$ if $j<0$ and therefore two ommatidia satisfy (for instance) Eq. (8).

With Fig. 4 we provide a generalized diagram for a neuro-ommatidium (in the upper half of the left eye, or for $j\geqq 0$). Here L_1 to L_4 represent lamina neurons and i^* and j^* indicate the relative indices of the ommatidia sending an axon to the considered neuro-

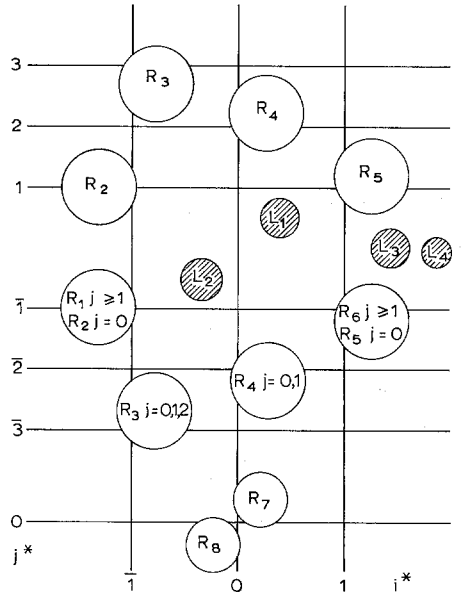

Fig. 4. Diagrammatic representation of a neuro-ommatidium (upper part of left eye). R_1 to R_8 indicate retinula cell axons; L_1 to L_4 are lamina neurons. The relative indices i^* and j^* represent the ommatidia indices delivering the respective photoreceptor cell axons; cf. Figs. 2 and 3

ommatidium. (For the sake of simplicity we have presented only four lamina neurons; cf. Braitenberg and Strausfeld, 1973.) The diagram of Fig. 4 may be compared with Fig. 4 of Horridge and Meinertzhagen (1970a). These authors have observed deviations from the normal situation concerning the location of retinal axons; for instance reversals of axons of R_3 and R_4 have been found, notably of axons entering from the other half of the eye.

Having arrived at this point we may conclude that neural positions as well as connections within the eye of the fly can be usefully described with the presented formalism. Yet, we wish to mention one more case, namely the connection pattern of the L_4 neurons in the lamina. It can be seen from e.g. Braitenberg (1970) and Braitenberg and Strausfeld (1973) that the connections of an L_4 neuron to adjacent neuro-ommatidia can be formalized with the aid of an operator $\boldsymbol{B}$ as follows:

$$\boldsymbol{B}\{L_4(i,j)\} = N(i + \operatorname{sign} i,\ j \pm \operatorname{sign} j)\,. \qquad (9)$$

This single example of a formal description of higher order neuron connections can be easily translated to other cases. Leaving that task to the future, we now turn to a case of more practical interest.

F. An Example: The Retinae of the Housefly *Musca domestica*

In order to visualize the ommatidial lattice of the fly we present as an application of the index notation in Fig. 5 the two retinae of a male wild type housefly Musca domestica.

The contour of both retinae has been charted by counting the ommatidia at the eye boundary. Each filled square in Fig. 5 represents an ommatidium. The equator, indicated by the white line, has been determined by utilizing the pseudopupil phenomenon (Kirschfeld, 1967; Franceschini, 1972). Actually the appearance of the cornea-pseudopupil (Franceschini and Kirschfeld, 1971) in the equatorial region resembles the different stages of Fig. 3 (cf. Kirschfeld, 1967).

In Fig. 5 we have furthermore indicated in both eyes those ommatidia which have their visual axes parallel to the vertical symmetry plane through the body axis of the fly. The angle between the visual axes of the successive ommatidia (given by a single point) has been (approximately) 10°. It can be derived from Fig. 5 that in the vertical symmetry plane the blind angle at the back of the head amounts to less than 100°.

Moreover we have indicated with a set of four points those ommatidia which have a visual axis parallel to that of a boundary ommatidium located in the other eye. The latter ommatidium has been denoted with a plain circle. Apparently the binocular region is less extended in forward directions than in directions inclined upwards and downwards.

In connection with the eye chart of Fig. 5 we may shortly point to a phenomenon occurring at the boundary of the eyes. From Eq. (6) it follows that the neuro-ommatidia have to outnumber the ommatidia, due to the spreading effect of the vector $\boldsymbol{s}_k$. Indeed, at the boundary of the lamina lattice there are located neuro-ommatidia with less than the usual neural elements shown in Fig. 4 (Boschek, 1971). For this boundary effect a formal solution must be found in order to preserve an unambiguous indication of the lattice points. This can be done in the following way: if one characterizes ommatidia with an index i, so that always $|i| > 1$, one avoids the possibility that two neuro-ommatidia located in different eyes obtain the same vector.

G. Discussion

We have presented a formalism for neuronal interrelations in the fly retina. An essential basis of this formalism is the H-V (respectively H* and V*) coordinate system together with the conjugated

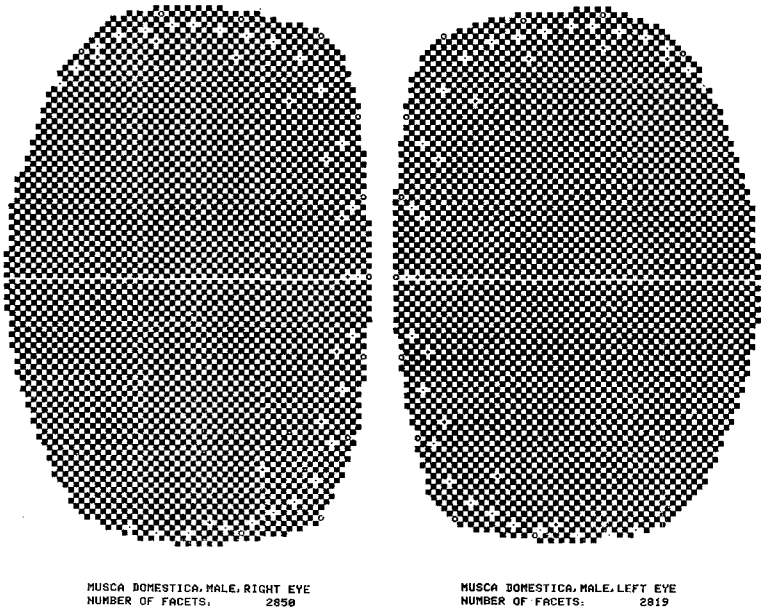

Fig. 5. The two retinae of a housefly *Musca domestica*. Each (filled) square represents an ommatidium. The white line indicates the equator. Those ommatidia having a visual axis (approximately) parallel to the symmetry plane of the body of the fly are given by a single point. The angle between the respective axes is (approximately) 10°. Ommatidia indicated by a set of four points have a visual axis parallel to that of a boundary ommatidium in the other eye. The latter ommatidium is given by a plain circle. Note the large binocular fields at directions inclined upwards and downwards

indices. The preference of such a system over the redundant and ambiguous system employing three or four axes which is used by Braitenberg and Strausfeld and co-workers (cf. Braitenberg, 1970; Braitenberg and Strausfeld, 1973) has been amply discussed in a separate paper (Stavenga, 1975).

Though we abstain from going into this matter thoroughly here, we refer to the most important findings of Kirschfeld (1972) who has shown that in the housefly motion detection occurs at successive stimulation of pairs of neuro-ommatidia $N^*(1, 1)$ and $N^*(1, \bar{3})$ respectively $N^*(1, 1)$ and $N^*(\bar{1}, 1)$; the latter pair is equivalent to $N^*(1, \bar{1})$ and $N^*(\bar{1}, \bar{1})$. It is especially this result which provides strong evidence for the fundamental value of the H-V coordinate system.

We still wish to discuss the property of these motion detectors of being affected by neighbouring neuro-ommatidia. Kirschfeld and Lutz (1974) conclude that the motion detector between $N^*(1, 1)$ and $N^*(\bar{1}, 1)$ exists in two forms to be called M_α^* and M_β^* respectively. M_α^* is inhibited by neural elements located in neuro-ommatidia $N^*(\bar{1}, 1)$, $N^*(1, 1)$ and $N^*(0, \bar{2})$. M_β^* is inhibited from neuro-ommatidia $N^*(\bar{1}, \bar{1})$, $N^*(0, 2)$ and $N^*(1, \bar{1})$. Remarkably, the detectors in each horizontal row are alternately of the α- and β-type. The same holds for vertical columns. The organization is such (in the frontal part of the upper half of the eye) that if $M_\alpha(i, j)$ holds then there exists $M_\alpha(i+4n+m,\ j+m)$ and $M_\beta(i+2+4n+m,\ j+m)$; n and m integer.

We have treated Kirschfeld's results with our formalism to show once more its feasibility and to indicate the way in which future revelations on neural interactions may be communicated.

Closely related to the optomotor studies of Kirschfeld are the electrophysiological experiments of McCann and Dill (1969) and McCann and Foster (1971) demonstrating motion detectors with extreme sensitivity in either the horizontal or the vertical direction. Also the behavioural investigations performed by Goetz (1968, 1972) have yielded results which point to orthogonally sensitive motion detectors.

Figures comparable to the example of the housefly retinae given by us in Fig. 5, have been obtained by Braitenberg (1967), Gemperlein (1969) and Braitenberg and Hauser-Holschuh (1972). A more detailed discussion on the latter reports in relation to our measurements on a series of other diptera will be presented elsewhere. Yet, from the experimental as well as from the theoretical examples presented here the essential benefit of the indices for a description

and further exploration of the fly visual system should be obvious.

Extrapolation of the formalism towards other insects is a straightforward matter, because insect visual systems are very similar in structure (Bullock and Horridge, 1965; Strausfeld, 1970a, b; Collett, 1972; Trujillo-Cenóz, 1972). Diptera are exceptional in having an open rhabdom which makes it possible to regard their retinula as a distinct lattice (cf. Fig. 1). Most insects have a closed rhabdom and hence it may not be feasible to assign different indices to their retinula cells. Still Eq. (1) holds also for bees, dragonflies and locusts et cetera if $\boldsymbol{q}_k = (0, 0)$ for all k. The chiasms occurring between lamina and medulla in insects then can be generally treated as a complete reversal of the direction of increasing i (Horridge and Meinertzhagen, 1970b; Strausfeld, 1971; Braitenberg and Strausfeld, 1973), the order in j meanwhile remaining unchanged.

Moreover, the formalism will be useful in the study of other invertebrates and even vertebrates. A regular structure in the vertebrate retina has been discussed repeatedly (cf. Schultze, 1866; Bouman, 1969; Bouman and Koenderink, 1972; Crescitelli, 1972; Wagner, 1972; Miller and Snyder, 1973). We may refer especially to Bouman (1969) who claims that the human retina is actually composed of ommatidia. To our knowledge, however, nowhere except in fly eyes has this regularity been preserved over the whole eye to such an astonishing perfection. This emphasizes that the fly visual system is a valuable "model for the processing of optical data in the nervous system" (Reichardt, 1971). The absence of a completely regular neural structure in other animals still implies no serious draw-back to our description scheme. The application of an absolute index system usually will indeed be questionable. All the same, we feel that small scale regularity can be exploited better in experimental practice. The proposed formalism utilizing relative indices can, we hope, be of some use in the further elucidation of both structure and function of the neural networks in visual systems.

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